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A REPORT ON THE TAXONOMIC STATUS AND DISTRIBUTION OF THE RED WOLF

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Abstract

Comparison of 213 skulls of Canis rufus with 214 C. lupus and 336 C. latrans indicates that the red wolf is a distinct species. In size and proportion, C. rufus appears intermediate between coyote and gray wolf, while certain trenchant cranial and dental details suggest coyote affinity. Before human disruption of the environment, rufus, lupus, and latrans maintained their distinct status, and available specimens show no evidence that the red wolf intergraded with either coyote or gray wolf.

A series of 71 skulls collected from the Edwards Plateau of central Texas in 1915-18 shows a complete range of variation from typical rufus to typical latrans. Apparently extensive habitat modification and decline of the red wolf population, both attributable to man, led to the breakdown of isolation and the formation of a hybrid swarm. Since only five specimens collected in other parts of the red wolf's range, prior to 1930, suggest possible interbreeding with the coyote, it is believed that a hybrid swarm occurred originally only in central Texas.

Specimens indicate that as red wolves were extirpated in eastern Texas and elsewhere, the swarm moved eastward to occupy the niche that was created. By 1969, the swarm had spread throughout most of eastern Texas and had moved into Louisiana. Pure red wolves continued to survive only in a limited area along the Gulf Coast from Brazoria County (east of the Brazos River) east to Chambers and Orange Counties, Texas, and in Cameron Parish.

INTRODUCTION

Hall and Kelson (1959) recognized three native species of North American Canis, based on the revisionary work of Goldman (Young and Goldman, 1944), and Jackson (Young and Jackson, 1951). These species are the gray wolf (Canis lupus), distributed from Alaska to Newfoundland and south into central Mexico, but absent over much of the southeastern and south-central United States; the coyote (Canis latrans), distributed from central Alaska into the north-central United States and south into Central America, but also originally lacking over most of the eastern and south-central United States; and the red wolf (Canis rufus), distributed from Florida to central Texas and north to southern Indiana and Missouri.

This concept of the speciation and distribution of North American Canis remained essentially unchallenged until Lawrence and Bossert (1967, p. 229), using a multivariate analysis, reported their findings as: "It now appears that the early populations described as Canis niger [=C. rufus floridanus] and n. gregoryi [=C. rufus gregoryi] from the southeastern wooded regions, east of the range of Canis latrans, are a local form of C. lupus, not a distinct species of wolf." Paradiso (1968) questioned the validity of Lawrence and Bossert's conclusions by pointing out that their small samples could not possibly encompass the wide range of geographic, individual, sexual, and age variation existing in the species under consideration, and that consequently the conspecific status of C. r. floridanus and C. r. gregoryi with C. lupus had not been adequately demonstrated.

We recently undertook an examination of all of the North American Canis material in the U. S. National Museum, as well as numerous specimens from other collections, in order to determine the taxonomic status and present distribution of C. rufus. We analyzed data on nearly 1,500 specimens, and the present paper is a report on our findings. All specimens are in the collections of the U. S. National Museum unless otherwise noted.

SAMPLING PROCEDURE

For the purposes of our study, we used comparative samples of C. lupus and C. latrans as defined by Young and Goldman (1944) and Young and Jackson (1951). We wanted these samples to cover as thoroughly as possible the wide range of geographic variation in both species, and consequently we selected subspecies of each from widely varied localities in North America. Within each subspecies, we selected a State or group of bordering States, and then measured and analyzed data on all adult specimens available from that particular geographic area. Age was determined by evaluation of suture closure, sagittal crest development, tooth wear, and season of collection.

Our sample of C. lupus consisted of 214 skulls representing seven subspecies from the following localities: C. lupus lycaon, Michigan 16, Minnesota 2, Wisconsin 1, New York 1, Ontario 1; monstrabilis, New Mexico 14, Texas 15, Tamaulipas 1; nubilus, Oklahoma 4, Kansas 3, Nebraska 16, Minnesota 2, South Dakota 10, Colorado 8; youngi, Colorado 13; irremotus, Idaho 22; baileyi, Arizona 15, Chihuahua 17, Durango 1, Sonora 1; pambasileus, Alaska 51.

The sample of C. latrans numbered 336 skulls and was drawn from six subspecies from the following localities: C. latrans mearnsi, Arizona 51; texensis, New Mexico 40; lestes, Idaho 128; latrans, Wyoming 60; incolatus, Alaska 30; thamnos, Iowa 1, North Dakota 3, Minnesota 5, Wisconsin 4, Michigan 8, Illinois 3, Manitoba 2, Ontario 1. We did not include in the sample any coyotes from within the original described range of Canis rufus.

In addition to these, we measured and analyzed data on all adult skulls in the U. S. National Museum from Texas, Oklahoma, Missouri, Arkansas, and Louisiana. These specimens had been previously assigned to the coyote subspecies texensis and frustror and to the red wolf. All adult specimens from this geographic region, which were obviously not typical coyotes or domestic dogs, were used in the red wolf sample. It was our objective to compare critically this sample with the samples of C. lupus and C. latrans in order to determine what differences and similarities existed between specimens from this geographic region and known series of gray wolves and coyotes.

Further comments are required with regard to the red wolf sample. As will be discussed later, it became apparent to us that the original canid population of the States from which the red wolf sample was drawn had been replaced by a different type of Canis within comparatively recent years. This replacement occurred in Arkansas, Missouri, and eastern Oklahoma sometime during the 1930's and in Louisiana during the 1940's. Since we were interested in determining the taxonomic status of the original canid population from these regions, we did not use in our standard sample any skulls taken in Arkansas, Missouri, and eastern Oklahoma after 1930, or any Louisiana specimens after 1940. Skulls from the extreme southeastern corner of Texas (see fig. 1) collected before 1944 show consistency within themselves and do not differ significantly in any way from the above-mentioned Arkansas, Missouri, eastern Oklahoma, and Louisiana specimens, and were included in the sample from the red wolf range. In addition, 5 skulls taken in 1900 in Calhoun County farther south along the Texas Gulf Coast were considered to be red wolves and were also included in the series. Seven coyotes were eliminated from these series on the basis of size, and nine specimens suspected of having domestic dog blood were not included. Such domestic dog characteristics as inflated frontal sinuses, short broad rostrum, short canines, and small premolar and molar teeth were used in eliminating such individuals. Our complete red wolf sample, when coyotes and suspected dogs or dog-hybrids were

eliminated, consisted of 213 skulls from the following States: Texas 30, Louisiana 21, Oklahoma 45, Arkansas 91, and Missouri 26. Of these, 23 were yearling animals used only in tabulating certain dental characters mentioned later. Other specimens previously identified by others as C. rufus included 1 from Florida and 3 from Alabama which were examined but not included in our sample.

Our red wolf sample, as listed above, was composed of two previously named subspecies. All specimens from Louisiana, and most from Arkansas and Missouri, as well as those from extreme eastern Oklahoma and Texas had been assigned by Goldman (Young and Goldman, 1944) to C. rufus gregoryi; specimens from the western edge of the range of C. rufus in Texas, Oklahoma, northwestern Arkansas and southwestern Missouri had been referred to C. rufus rufus. McCarley (1962) suggested that since C. r. rufus was a smaller, lighter built subspecies than C. r. gregoryi, the entire taxon might be only a hybrid C. latrans x C. rufus. However, specimens collected in Texas to the west of Galveston Bay, as shown in figures 1 and 2, indicate a natural shift to slightly smaller, narrower skulled animals. Yet these specimens show no evidence of intergradation with the much smaller coyote found further south and west. The characteristics of the red wolf here have been maintained from 1900 (when we first have specimens from the area) to the present day. Although a large part of the recognized geographic range of C. r. rufus was indeed occupied by a hybrid form (as will be discussed later), we do not agree with McCarley's suggestion that the entire taxon C. r. rufus represents hybridization between the red wolf and the coyote. Figures 1 and 2 show the locations by counties for all specimens of C. rufus in our standard sample. These figures also show the distribution of all specimens of other Canis in the U. S. National Museum taken before 1943 in Texas, Oklahoma, Missouri, and Louisiana.

MEASUREMENTS AND CHARACTERS

In the course of our study, we used many measurements and ratios in an attempt to identify taxa. The great amount of intraspecific variation, and the broad overlap in most structural features among samples forced us to reject most measurements as useless for our purposes. We found that the measurements, ratios, and dental characters as defined below had the least amount of intraspecific variation and species overlap, and provided the most clearcut distinctions between taxa. The mean, the extremes, one standard deviation, and two standard errors on either side of the mean show these distinctions.

Five measurements and two ratios derived from three of the measurements were taken from each skull used in the study. In addition, unmeasurable dental characters were observed in each specimen. Two measurements used directly were:

Greatest length of skull--distance from the posteriormost projection of the sagittal crest to the anterior tip of the premaxillae.

Zygomatic breadth--greatest distance across zygomata.

The ratios derived from the three additional measurements were the following:

Bite ratio--the reciprocal of the width across the outer edges of the alveoli of the anterior lobes of the upper carnassials, divided by the length of the upper molar toothrow from the anterior edge of the alveolus of Pm^1, to the posterior edge of the alveolus of M^2. We have found that a high bite ratio is correlated with a relatively massive skull in Canis and is directly associated with strong maxillary and premaxillary development.

Upper M^2 ratio--the reciprocal of greatest width of upper M^2 measured diagonally, divided by the zygomatic breadth.

In our material five unmeasurable, trenchant dental characters were found to be less variable in time and space than the measurable ones listed above and those used by Lawrence and Bossert (1967). The pertinence of some of these in distinguishing lupus from rufus was pointed out by Goldman (Young and Goldman, 1944). We feel that they are strongly indicative of relationships. They are as follows:

1. Length of canines in relation to anterior mental foramina when the jaws are closed. In our analysis, we gave a positive reading to any specimen in which the canines extended below the anterior mental foramina when the jaws were closed. Only adults were used when appraising this character.

2. Presence of prominent cingulum on the outer side of upper M^1. A positive score was given if the cingulum was developed enough to form a distinct ridge that could be felt in running a fingernail down the side of the tooth. Yearlings as well as adults of C. rufus and C. lupus were tabulated for this and the following three dental traits to increase the sample size.

3. Development of distinct deuterocone on upper Pm^4. A positive reading was given if the height of the deuterocone extended above the ridge connecting it to the rest of the tooth.

4. Deeply cleft crowns and laterally compressed cusps of the large upper molariform teeth. When the crowns are deeply cleft and cusps are laterally compressed, deep molar "sculpturing" is immediately apparent. If this "sculpturing" was pronounced, the specimen was rated positive.

5. Development of metaconule on upper M^1. We tabulated this as positive if the metaconule had any development at all.

It is obvious that some of the unmeasurable characters listed above are subjective in nature and that our judgement in rating them had to be arbitrary. Both authors listed ratings independently, and in nearly all instances there was agreement between ratings.

In the course of our investigations, we examined series of skins of C. lupus, C. latrans, and C. rufus. There is so much geographic, individual, and seasonal variation in the pelages of all three species, that is is impossible to assign most individual specimens to species on the basis of coloration alone. Consequently, we do not consider pelage to be a specific character and have not included it in our analyses.

RESULTS

Canis latrans and C. lupus

C. latrans is readily separable from C. lupus in all instances. There is no overlap in zygomatic breadth, greatest length of skull, or bite ratio between the largest C. latrans and the smallest C. lupus (figs. 4-8). In addition, in numerous cranial and dental details the two samples have pronounced differences in frequency of characters. The sagittal crest in lupus is nearly always well developed but that in latrans is usually not. This is a direct reflection of the strength of the jaws and difference in feeding habits of the two species. Inflation of the frontal region of lupus is generally prominent, but that of latrans is flat; the rostrum of lupus is short and heavy, but that of latrans is long and slender. The coyote has an inflated braincase, with maximum width in the region of the parietotemporal suture, whereas in the gray wolf the maximum width is usually at the roots of the zygoma. In table 1, various unmeasurable differences in the dentition of C. lupus and C. latrans are evident when the frequency of occurrence of each character is compared between the two samples.

C. rufus and C. lupus

There is no question that C. lupus and C. latrans are distinct at the specific level, but C. rufus is confusing because in many ways it is intermediate between the two. It can be seen (figs. 4-7) that in greatest length of skull and, to a lesser extent, in zygomatic breadth, that C. rufus approaches C. lupus. Goldman (Young and Goldman, 1944) and Lawrence and Bossert (1967) mentioned

other resemblances between the two species. Lawrence and Bossert nevertheless failed to consider some of the key characters of the skull and dentition in which C. rufus falls closer to C. latrans than to C. lupus. Generally speaking, we have found the red wolf to be a much less massive animal than the gray, with lighter, more narrowly spreading zygomata, relatively flat frontals, more delicate dentition, and a considerably weaker rostrum reflected by lighter maxillary and premaxillary development. These differences are in most instances readily apparent to the eye, and the majority of specimens can be separated on this basis alone. The less massive structure of the skull of C. rufus is best reflected in the bite ratio (fig. 8). This ratio clearly does not indicate in itself that C. rufus is closer to C. latrans than to C. lupus, but it does show that the rufus series has a strong consistency within itself and is significantly distinct from the other two species.

The more massive structure of the gray wolf's skull is not a function of its greater average size. The two largest C. rufus skulls that we examined are from Garland County, Ark., and Madison Parish, La., and measure 261 mm and 250 mm in greatest length. Both are remarkably narrow, and they have bite ratios of 76.6 and 75.1. In contrast, skulls of the smallest gray wolf, subspecies C. lupus baileyi, are broad, and its average bite ratio is 87.3 (figs. 4-8).

There is an increased development in the size of the two upper molars in the red wolf as compared with the gray wolf. The last upper molar in fact often has a larger absolute size in the red wolf than in the gray wolf, and is usually much larger in proportion to size of skull. The red wolf is closer to C. latrans than to C. lupus in this respect. The three species are compared for this feature in figure 9.

The fact that C. latrans has an inflated braincase, generally with maximum width in the region of the parietotemporal suture, while in C. lupus maximum width is usually at the roots of the zygoma, is a good way of separating most coyotes from gray wolves. Some C. rufus, however, approach C. latrans in this character, and most are in between coyote and gray wolf. In addition, some coyotes also have maximum braincase width at the base, and these specimens are the ones which also have the greatest zygomatic breadth and the best developed sagittal crest. All of these features are related and associated with the overall massiveness of the skull.

Table 1 shows differences between samples of C. rufus and C. lupus with regard to the five unmeasurable dental characters.

It has occasionally been reported (as by Young and Jackson, 1951) that in C. rufus the canines do not extend below the level of the anterior mental foramina when the jaws are closed, and that this feature could be used to distinguish the red wolf from the coyote in

which the canines do extend below these foramina. By actual count we have found this not to be the case (table 1). In length and structure of canines, C. rufus resembles C. latrans more than it does C. lupus.

It can be seen from figures 4-9, and table 1, that of the several subspecies of the gray wolf, the subspecies C. l. lycaon most closely resembles the red wolf in measurements, ratios, and dental characters. Goldman remarked on this resemblance in some individuals of the two taxa as concerns overall size and proportion. Nevertheless, C. l. lycaon still clusters closely with the other subspecies of the gray wolf, and there is no evidence that the characters of C. rufus change toward those of lycaon from south to north. Indeed, a good series of red wolves from Missouri, just to the southwest of lycaon's range, is consistent with a series from Louisiana (figs. 4-9 and table 1) in almost all measurements, ratios, and dental characters. The shift of lycaon toward rufus probably represents convergent evolution due to similarity of habitat and general lack of competition with other species of Canis.

From our data it appears that C. rufus differs more from the western subspecies of C. lupus than it does from C. lupus lycaon. One specimen of C. l. monstrabilis from Texas has a bite ratio of only 79.0, but in size (greatest length of skull) and other morphological features discussed it differs notably from C. rufus just to the east.

There is even more difference between C. rufus and C. l. nubilus of the Great Plains. Our series of nubilus from Oklahoma, Kansas, Colorado, Nebraska, South Dakota, and Minnesota shows no tendency to intergrade with the large red wolf series from Missouri, Arkansas, and Oklahoma (figs. 4-9 and table 1). In animals as large and as mobile as wolves, it would be rather surprising to have such a substantial shift in characters over so small a distance with no geographic barrier, if only one species were involved. Because of the ease of separation of nearly all specimens of C. rufus from C. lupus and because of the lack of any positive evidence of intergradation between the two in nature, we regard C. rufus and C. lupus as two species.

Throughout its circumpolar range, C. lupus is primarily in areas which have a cold season for part of the year. In North America it did not inhabit most of California, Baja California, and the Mexican lowlands (Young and Goldman, 1944). In contrast, the red wolf was found along the Gulf Coastal Plain and even in Southern Florida. Goldman listed immature C. rufus specimens from Wabash County, Ind., and from Hancock County, Ill., and he thus mapped northward range extensions for the species. The Indiana specimen, however, was actually from the Wabash River area in the southern part of the State as it was correctly located by Lyon (1936) and Mumford (1969).

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The Illinois skull was possessed by an animal dealer in Hancock County and apparently was from a captive wolf (E. Raymond Hall, pers. comm.). We therefore believe that C. rufus is essentially a warmth-adapted species in contrast to the more cold-adapted C. lupus.

C. rufus and C. latrans

Canis rufus resembles C. latrans more than it does C. lupus in all of the unmeasurable dental characters listed in table 1, and in the upper M^2 ratio (fig. 6) and in general shape of skull. Both latrans and rufus have long slender rostra with distinctly flattened frontal regions and narrowly spreading zygomata.

Nevertheless, comparison of our standard series convinces us that the two are sufficiently distinct to warrant full specific recognition. Indeed, because they differ so greatly in size, it is generally easier to differentiate between them than between lupus and rufus which differ less obviously in structural details. Visually it is quickly apparent that rufus has heavier bone structure and dentition, the skull is relatively broader, and there is a much more pronounced sagittal crest.

The most reliable feature separating latrans from rufus is lesser size (figs. 4-7). There is almost no overlap in greatest length of skull in our standard samples when considering animals of only one sex. In the course of our study, we examined each of the thousands of coyote skulls in the U. S. National Museum, and found only two males in which the greatest length exceeded that of the smallest male of C. rufus. These two were from South Dakota, subspecies C. l. latrans, and each has the narrow shape and light dentition of typical coyotes, as well as low bite ratios (69.9 and 74.5).

The differences between coyote and red wolf are far greater than any variation exhibited by any recognized subspecies of C. latrans over its entire range (figs. 4-9). Even a large series of coyote skulls from Tom Green County, Texas, adjacent to the former red wolf range, show no shift toward C. rufus in size or bite ratio (figs. 10-12). Because of this, and because of the fact that our specimens indicate that they occurred sympatrically in some places (as will be discussed later), we conclude that C. rufus is specifically distinct from C. latrans.

SYMPATRIC DISTRIBUTION OF RED WOLF AND COYOTE

The coyote and red wolf were primarily allopatric species. The range of C. latrans included the drier regions and grasslands of the west, along the edge of the eastern forested zone (Young and Jackson, 1951). Its range extended as far east as Indiana, but never far distant from the prairies (Lyon, 1936). C. rufus, on the other hand, was found mainly in more humid regions of predominately forest type. It originally occupied the southeastern forests, swamps, and coastal marshes, and extended some distance up the wooded river valleys and through the more broken woodlands of Texas and Oklahoma.

Despite the fact that the two species were primarily allopatric, there appear to have been areas in the western part of the red wolf's range where the two did overlap in distribution, and in these areas we have evidence that they maintained themselves as distinct species without extensive interbreeding. For instance, from southern Missouri there is a series of 26 typical red wolves in the National Collection taken between 1920 and 1925, and these compose the Missouri portion of our red wolf standard samples (figs. 4-9). From this same period and area (fig. 1) we have five typical coyotes which range from 182.4 to 208.3 mm in greatest length of skull, from 90.2 to 105.9 mm in zygomatic breadth, and from 65.6 to 69.5 in bite ratio. We feel that C. rufus and C. latrans occurred sympatrically here, and there is no evidence of any intermediate forms.

From Arkansas during the period 1919 to 1928, we have a large series of typical red wolf skulls (composing the Arkansas segment of our red wolf series graphed in figs. 4-9), and only two specimens from that State during this period appear to be unusual. These are two females from Newton County which have greatest skull lengths of 191.4 and 200.6 mm but bite ratios of 77.9 and 78.6 and heavy bone structure. We did not include these in our standard red wolf sample. We also have two typical C. latrans from the same time and area: males with greatest lengths of 199.3 and 204.5 mm and bite ratios of 72.0 and 69.7. We also know, from Audubon and Bachman (1851), that coyotes were common in the northwestern areas of Arkansas, and we believe that if coyotes and red wolves were freely interbreeding there we would have a greater representation of intermediate animals in our collection.

A series of 22 specimens in the National Collection from central and western Oklahoma (Comanche, Tulsa, Creek, and Tillman Counties) and one adjacent north Texas County (Hemphill), taken in the period 1902 to 1905, is clearly typical C. latrans, ranging from 181.9 to 204.8 mm in greatest length of skull, 88.7 to 106.3 mm in zygomatic breadth, and 66.9 to 74.1 in bite ratio. Three specimens taken in the same period in Tulsa and Coal Counties are clearly red wolves and were included in our standard sample. One earlier

specimen from Garvin County in south-central Oklahoma is also typical C. rufus. There is no evidence of any intermediate forms. A much larger series of Oklahoma specimens collected from four southeastern counties (McCurtain, Atoka, Le Flore, and Pushmataka) from 1919 to 1928 forms the bulk of our standard red wolf sample from that State. Only two specimens from this area and period are questionable as to identity. Both are from McCurtain County. One is a male which measures 204.2 mm in greatest length of skull and 108.3 mm in zygomatic breadth and has a bite ratio of 74.6. This animal may well have been a large coyote. The other questionable specimen is a female with greatest length of skull measuring 204.7 mm, zygomatic breadth 106.9 mm, and a bite ratio of 79.9. These specimens were not included in our standard sample. During this same period a series of 11 specimens from the western part of the State (Custer and Canadian Counties) are all typical latrans, ranging from 181.0 to 207.6 mm in greatest length of skull, from 90.4 to 106.1 mm in zygomatic breadth, and from 65.0 to 72.2 in bite ratio.

In Texas, 26 specimens taken from 1891 to 1902 in Nueces County on the Gulf Coast range from 180.2 to 208.8 mm in greatest length of skull, 90.1 to 104.4 mm in zygomatic breadth, and 65.0 to 77.3 in bite ratio, all well within the size range of our standard coyote sample. Only 75 miles up the coast in Calhoun County, 5 specimens taken in 1900 are typical red wolves with greatest length of skull ranging from 220.0 to 237.1 mm. One female specimen, however, measures 202.1 mm in greatest length and 105.4 mm in zygomatic breadth, with a bite ratio of 78.4, and may represent a hybrid. Considering the mobility of these canids, we feel there would certainly have been greater evidence of intermediate types in the two series if C. rufus and C. latrans were interbreeding extensively.

The above examples indicate to us that, even as late as the 1920's, there was a clear separation between C. rufus and C. latrans in most areas where their ranges approached or overlapped. The fact that there are only 5 questionable specimens in the same areas as 213 consistent C. rufus skulls, long after the coming of the white man and the initiation of extensive environmental changes, suggests to us that a hundred years earlier the two species were completely distinct throughout their entire ranges.

HYBRIDIZATION BETWEEN RED WOLF AND COYOTE

Although the eastern subspecies of the red wolf (Canis rufus floridanus) was extirpated at an early date, it was long believed that C. rufus was still abundant west of the Mississippi. McCarley (1959, 1962) was the first to call attention to the fact that the species might be bordering on extinction even in this region. This viewpoint was later supported by Paradiso (1968).

We think man played the major role in bringing about the decline of the red wolf. Among the detrimental factors attributable to man were the cutting over of forest habitat, construction of wolfproof fences, extensive hunting by ranchers and farmers, the bounty system, and State and Federal control operations. All these factors seem to have reached a peak by the 1930's. Nearly all our museum specimens from Texas, Oklahoma, Arkansas, and Missouri from about the first two decades of the present century are large red wolves. But specimens obtained since about 1930 are a much smaller and different kind of canid.

In Missouri, the combination of unfavorable environmental factors brought about the decline of the red wolf by about the mid-1930's, and it was rapidly replaced by coyotes. The skull of a male in the National Collection, taken in 1932 in Iron County, has a greatest length of 219.6 mm and a bite ratio of 79.3. This animal may have been one of the last red wolves in the State. In the National Museum, all Missouri specimens collected after 1932 are coyotes. Sampson (1961), who reported on Missouri specimens, including some not in the National Museum, recorded a few intermediate specimens taken in this State from 1932 to 1942, but almost all taken after this period were coyotes.

Three specimens from eastern Oklahoma, taken in 1932, are as follows: Cherokee County, female, greatest length 211.6 mm, zygomatic breadth 105.0 mm, bite ratio 75.6; Atoka County, female, greatest length 214.2 mm, zygomatic breadth 106.5 mm, bite ratio 73.4; Le Flore County, male, greatest length---, zygomatic breadth 109.2 mm, bite ratio 71.5. These skulls are all just within the lower limits of our standard red wolf sample. McCarley (1962) reported two large skulls, taken in McCurtain County in 1936, as red wolves. Possibly, then, the red wolf maintained itself as a genetically pure population in Oklahoma into the 1930's.

But we also have three males taken in Cleveland County in central Oklahoma in 1932 having greatest lengths and bite ratios of 217.3 mm, 66.0; 202.2 mm, 73.2; 208.0 mm, 67.4. There is thus some hint of a shift toward animals intermediate in nature between coyotes and red wolves at this time. McCarley (1962) found that ten skulls collected since 1949 from four eastern Oklahoma counties were intermediate in size between typical C. latrans and C. rufus. We have examined a series of 65 skulls collected from central and western Oklahoma from 1932 to 1942 and all are typical C. latrans. Paradiso (1968) reported only C. latrans from series collected since 1962 in eastern Oklahoma.

Apparently, then, in Missouri and Oklahoma there was a minimum of hybridization. The large red wolves present in the 1920's were gone by 1940 and their place had been taken by coyotes. There was not a gradual dilution of a gene pool through hybridization

resulting from long-term ecological changes. Rather there was the extermination of a dominant carnivore followed by an influx of another species to fill it ecologic niche.

Although the evidence indicates that red wolves were rapidly replaced by pure coyotes in Missouri and Oklahoma, with hybridization being minimal and having little effect on the present canid population, the situation is different in Texas, Louisiana, and parts of Arkansas. Here, the great morphological diversity of the present canid population indicates that hybridization must have played a major role in its formation. Animals from these areas range in size and other characters from typical red wolves to typical coyotes, with both extremes and intermediates occurring together. Goldman (Young and Goldman, 1944) mentioned that some Texas specimens he examined appeared intermediate between red wolf and coyote, and he considered them hybrids. Paradiso (1968) considered the canids of most of eastern Texas to comprise a single interbreeding population of hybrid animals. He supported the theory proposed by McCarley (1962) that extensive hybridization between red wolves and coyotes may have resulted from extreme habitat changes induced by man, but felt that decimation of pure red wolf populations may also have been a factor in this phenomenon.

We now feel that both of these factors may have brought about limited hybridization between red wolves and coyotes in some areas, but that the only area in which extensive hybridization occurred, and was to have an important effect, was in the Edwards Plateau area in central Texas. It seems to us that this area was a likely place for the occurrence of such extensive hybridization. The Edwards Plateau area contains extremely varied and intermingled habitat ranging from densely forested river valleys, through sheltered canyons and prairies, to arid stony slopes. In the area there was a mixture of life forms, the valleys being extensions of the eastern woodlands, while the surrounding sectors represented the typical western semiarid zone (Bray, 1904).

Under original conditions in this area, relatively dense populations of red wolves and coyotes maintained themselves as distinct species. The coming of the white man brought disruption of the existing habitats. All wild canids were killed as predators at every opportunity, with the larger red wolf being the hardest hit. Simultaneously there was clearing of the river forests, cultivation, introduction of livestock, and construction of wolfproof fences. Overgrazing soon led to the decline of the grasslands and the rapid spread of mesquite (Bray, 1904). Such disruption would have led to a pronounced breakdown of ecological isolation and an unprecedented contact between species such as C. rufus and C. latrans.

There are no specimens representing this area (or any other involved in the present problem) from the period before habitat modification. We have a series of 63 skulls taken from the central Texas counties, and from western and southern parts of the State, in the period of 1890 to 1906. Since most of these are unsexed, they are not comparable statistically with our other series and have not been plotted in our figures. Fifty-three of the skulls are from El Paso, Maverick, Irion, Terrell, Ward, Cameron, Kleburg, Jim Wells, and Nueces Counties in the western and southern parts of the state. These are skulls of typical coyotes, ranging from 179.2 to 208.8 mm in greatest length of skull, and from 65.1 to 77.3 in bite ratio. We also have ten skulls taken from the three adjoining counties of Edwards, Kerr, and Gillespie in the heart of the Edwards Plateau. These skulls give evidence of being intermediate between red wolves and coyotes. Males range in greatest length of skull from 207.0 to 219.8 mm, and the bite ratios of the 10 specimens are 69.5, 71.0, 71.6, 72.5, 73.4, 73.7, 73.9, 76.0, 77.0, and 77.0.

Much larger Texas series are available from the years 1915 to 1918 and largely represent the heavy initial take by the predator control program. Examination of these specimens shows that C. latrans occurred consistently, with no evidence of red wolf influence, over the prairies and arid regions of western and southern Texas. However, from the region of the Edwards Plateau and just to the north there are specimens which show an entire range of characters from typical coyote to red wolf. Figures 10, 11, and 12 show how all of these specimens compare in greatest length of skull, zygomatic breadth, and bite ratio with our combined standard coyote and red wolf samples. We have also tabulated data from a large series of specimens from Tom Green County which is adjacent to the area where extensive variation begins (fig. 1).

The graphs show no significant differences between the standard coyote sample and the specimens from western and southern Texas. Even the series from Tom Green County, at the very edge of the former range of the red wolf, exhibits no divergence from typical C. latrans. There is thus no hint of the gradual change in characters that would be expected if two large mobile populations of mammals were undergoing subspecific intergradation.

We have, in addition, included data on our graphs for skulls of C. lupus monstrabilis, which formerly occurred in the same region (figs. 10-12). These specimens show no overlap whatsoever with the hybrid group, and thus provide further evidence that C. latrans was not interbreeding with the gray wolf, but with another entity to the east, C. rufus. Counties in which specimens of C. l. monstrabilis were taken between 1900 and 1917 are shown in figure 1.

One specimen of coyote from western Texas deserves special comment. Goldman assigned a skull from Pecos County to C. rufus and thus extended the range of the species into this area. We have examined this specimen, and although it is heavily structured for a coyote, it has an overall length of only 207.3 mm and a bite ratio of 75.4. In other features it is hardly distinguishable from a few skulls of C. latrans lestes from Idaho. We consider it to be a large C. latrans and do not believe the range of the red wolf ever extended so far west as Pecos County.

To the east of Tom Green County, specimens differ greatly in size, although the bite ratio hardly exceeds the standard coyote average (figs. 10-12). The group is composed of 71 adults collected between 1915 and 1918 from Menard, Sutton, Llano, Concho, Coleman, Burnet, San Saba, and Blanco Counties. In general the skulls from this area are closer to those of coyotes, but some fall clearly within the size range for C. rufus, while others span the entire character gradient between the two species. The different forms are scattered throughout the area in no geographical pattern. It seems impossible to distinguish species in this area by means of size, structure, ratios, or dental features. The specimens from this area had been previously labeled as either C. latrans texensis, C. latrans frustror, or C. rufus rufus, and presumably had been identified by Goldman. Some skulls identified as coyotes, however, are larger and more massive in every way than others labeled red wolves. We believe that these names have no validity here, and that the specimens represent a hybrid swarm. Figure 1 shows the location of all C. latrans, C. rufus, and hybrid forms in Texas during this period.

Goldman recognized that hybridization was occurring in this area, but he felt that it was relatively restricted and that most specimens could be separated. We disagree; this series forms a gradual transition which cannot properly be broken at any one point. We have applied Goldman's criteria for distinguishing the two species, and they are not valid in this area. We have also examined available skins from this time and area and have seen no characters to distinguish the two species.

This hybrid swarm apparently formed first in central Texas and then spread to the east and filled the niches created by man's disruption of the habitat and extermination of the red wolf. A massive breakdown of ecological isolation and greatly increased gene exchange along the former border between C. rufus and C. latrans did not necessarily develop. Rather, our evidence indicates a geographic expansion of the hybrid animals themselves, reinforced by a constant movement of C. latrans to the east, into a niche left vacant by the decimation of C. rufus. There is no indication that hybridization occurred to a large extent anywhere except in the central Texas area, where the peculiar natural conditions of "eastern" and "western" habitat types supported the phenomenon.

A series of skulls collected in east-central Texas from 1932 to 1942 is represented in figure 13. The specimens illustrate the eastward movement of the hybrid zone and the replacement of the original C. rufus population in this area by a different entity. Figure 2 shows the localities from which these specimens came. This series does not include the extreme southeastern Texas counties already discussed where true C. rufus apparently persisted until at least 1944. The six previously discussed intermediate specimens collected in Oklahoma in 1932, and a series of 10 intermediate Arkansas skulls collected between 1932 and 1942, are also depicted by county on figure 2.

Paradiso (1968) reported on 279 wild Canis skulls taken after 1962 in eastern Texas. These specimens represented the entire collection assembled by the Bureau of Sport Fisheries and Wildlife since the renewal of Federal interest in the problem. It was found that on the basis of size (greatest length, condylobasal length, zygomatic breadth), these skulls are structurally intermediate, and span the entire gap between typical C. latrans and C. rufus. Specific data were presented for adult males only.

In our study, a more extensive analysis of the east Texas material was made. The counties in which these specimens were taken are indicated in figure 3. Figures 14 and 15 show the size range of the adult males and females in this group, and the combined bite ratio, as compared to our standard red wolf and coyote samples. Zygomatic breadth was not plotted because it has no significance not demonstrated by greatest length of skull alone. It is again apparent that we are dealing with a population intermediate in size between C. rufus and C. latrans, although averaging closer to C. latrans. The bite ratio of the new material shows only a slight increase above that of typical coyotes. In development of the sagittal crest these specimens are intermediate between the parent species. Essentially, then, these skulls that were newly collected in east Texas show the same range of variation that was found in the series of specimens taken from central Texas in 1899 to 1918, and east-central Texas in 1932 to 1942. It is thus indicated that the hybrid swarm, which initially formed in central Texas at an early date, has now engulfed the eastern part of the State. The fact that animals from the hybrid swarm have been consistent in their characteristics from 1899 to the present (compare figs. 10-15) indicates that the swarm represents an expanding entity rather than a gradual dilution of the red wolf gene pool.

In Louisiana, pure red wolves persisted up until about 1940. All specimens from the State before that year are consistent in showing red wolf characters, and comprise the Louisiana portion of our red wolf standard series. In 1938, U. S. Biological Survey trapping began in Louisiana, and an intensive State control program began in 1946. By 1950, the red wolf, as a pure population, was

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largely restricted to the eastern bottomlands and coastal marshes of the State (Nowak, 1967, 1970). But beginning about 1949, a new form of Canis was recognized as moving into Louisiana from the northwest. This form was clearly smaller and apparently more adaptable to broken habitat. These smaller animals did not gradually take over from C. rufus, with a steady reduction of red wolf characters in the original population; rather it appears to be a case of the initial extermination of the red wolf, and then geographical invasion of the area by the other form. We feel that this form represents the expansion of the Texas hybrid swarm, filling the void left in Louisiana by the intensive control of the red wolf.

A series of 27 skulls of Louisiana Canis collected from 1963 to 1969 was examined by us. The greatest length of skull for this series ranges from 190.0 to 221.5 mm, with zygomatic breadth ranging from 93.7 to 110.4 mm. Although these specimens were mostly unsexed. they nevertheless show the same size variation as animals of the hybrid swarm in Texas.

Paradiso (1968) reported only coyotes existing currently in Arkansas. Examination of 42 canid skulls collected in 1964 from this State shows a slight hybrid influence in that four males from Little River, Chicot, and Hempstead Counties (located on fig. 3) appear significantly larger than coyotes (greatest lengths: 212.8, 214.6, 215.0, 222.3 mm). Sealander and Gipson (1969) also report finding a few intermediate skulls, but mostly typical C. latrans in Arkansas. Apparently, then, the hybrid swarm never became well established this far north and may now be losing influence.

PRESENT DISTRIBUTION OF THE RED WOLF

Pure populations of C. rufus existed, as of 1969, in certain sections of extreme southeastern Texas (fig. 3). Pimlott and Joslin (1968) said that they located several packs of red wolves in Chambers County by means of vocal recognition. Paradiso (1965) reported several specimens collected in 1963 or 1964 in Chambers County that did not significantly differ from C. rufus. This evidence, plus numerous local reports, led to a Bureau of Sport Fisheries and Wildlife field study in the six southeastern Texas counties of Brazoria, Galveston, Chambers, Liberty, Jefferson, and Orange, from March 1968 until June 1969 by John L. Steele, Jr. He reported locating pure populations of C. rufus over much of the study area, but noted that they were greatly endangered.

Series of specimens collected in 1969 in southeast Texas have allowed us to estimate more closely the range of C. rufus at that time. One series of 32 skulls, taken by a private hunter, was sent from a locality in Brazoria County, west of the Brazos River.

Although most of these specimens are unsexed and immature, it is evident that they represent the variation shown by the canid population over most of eastern Texas. Hence the hybrid swarm seems to be established in western Brazoria County.

The situation east of the Brazos River as of 1969 was different. We have examined a total of 18 skulls of canids from Brazoria County, east of the Brazos River, and 17 skulls from Chambers, Jefferson, and Liberty Counties, all collected between 1963 and 1969. Data on sexed adults from this material are plotted in figures 14 and 15, and compared with our standard red wolf and coyote samples and the series of hybrids from the remainder of eastern Texas. These specimens show a strong shift away from latrans and towards rufus in greatest length of skull, and bite ration. In addition, unmeasurable features of the dentition, sagittal crest development, and frontals show no deviation from typical C. rufus. Ten of the specimens from these coastal counties are unsexed and have not been used in the figures, but they are also large and indistinguishable from specimens in our red wolf sample. They range from 212.2 to 246.2 mm in greatest length of skull, with zygomatic breadth ranging from 107.8 to 126.5 mm. Eleven specimens from Brazoria County and one from Chambers County are yearlings, but they are also much larger than even adult coyotes or specimens from the hybrid swarm. They range from 209.2 to 219.2 mm in greatest length of skull, and from 101.5 to 117.5 mm in zygomatic breadth.

Interestingly, the specimens from eastern Brazoria County and those from Chambers and Jefferson Counties appear to represent the survival of the two described subspecies C. rufus rufus and C. r. gregoryi. Although the series are small, the Brazoria County specimens have the narrower and lighter skull that is typical of all material from the Texas coast, west of Galveston Bay, since the earliest specimens were saved. In contrast, the new Chambers and Jefferson County skulls are heavier and broader as in specimens collected earlier from the same region and farther east. The two populations were actually well separated by Galveston Bay and the densely settled Houston area.

The expansion of the Houston metropolis is only one of many factors threatening these last red wolves. Habitat changes and continued human persecution may destroy the viability of these remnant populations and permit a complete takeover by the hybrid swarm (Nowak, 1970).

Recent field work by Pimlott and Joslin (1968) located possible red wolf populations in northeastern Louisiana and the Ozark National Forest of Arkansas, but we have no specimens to confirm these findings. A single skull, identified as C. rufus, was reported by Pimlott and Joslin to have been taken in St. Landry Parish in south-central Louisiana. One of us (Nowak) recently visited a

ranch in Cameron Parish, southwestern Louisiana, where he saw the mounted heads of two large canids, collected sometime in the period 1963 to 1965, which he considered to be red wolves. These specimens, plus other reports from southern Louisiana, lead us to believe that a small number of red wolves may survive in that area.

Thus, it appears that in the former range of the red wolf in Missouri, and eastern Oklahoma, the species has been replaced by coyotes; in much of east Texas, Louisiana, and perhaps parts of Arkansas, it has been replaced by a mixed hybrid swarm that originated on the Edwards Plateau before the turn of the century and now ranges far to the east.

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Table 1.--Percent of positive development of various dental characters in populations of C. lupus, C. rufus, and C. latrans. Figures in parentheses indicate sample size. See text for explanations.

	CANINE LENGTH	CINGULUM DEVELOPMENT	DEUTEROCONE DEVELOPMENT	DEEP UPPER MOLAR TOOTH SCULTURING	METACONULE DEVELOPMENT
LUPUS					
pambasileus	7% (30)	19% (48)	16% (50)	10% (49)	65% (48)
irremotus	0% (11)	9% (21)	5% (21)	0% (20)	48% (21)
youngi	0% (7)	0% (12)	17% (12)	0% (12)	83% (12)
baileyi	0% (10)	6% (33)	18% (33)	0% (33)	24% (33)
monstrabilis	5% (18)	10% (29)	7% (30)	0% (30)	40% (30)
nubilus	2% (21)	7% (43)	22% (45)	0% (43)	28% (43)
lycaon	40% (15)	24% (21)	14% (21)	9% (22)	59% (22)
Total LUPUS	12% (112)	12% (207)	15% (212)	3% (209)	46% (209)
RUFUS					
Missouri	65% (20)	70% (23)	84% (25)	54% (24)	96% (25)
Oklahoma	48% (36)	91% (44)	77% (44)	66% (44)	93% (44)
Louisiana	67% (12)	76% (21)	52% (21)	86% (21)	95% (21)
Arkansas	68% (62)	77% (88)	70% (88)	54% (91)	94% (88)
Texas	48% (25)	71% (28)	79% (29)	93% (27)	100% (27)
Total RUFUS	63% (155)	78% (204)	73% (207)	65% (207)	95% (205)
LATRANS					
thamnos	86% (21)	96% (24)	92% (26)	100% (25)	100% (25)
texensis	97% (31)	72% (39)	79% (39)	97% (38)	100% (39)
mearnsi	92% (38)	57% (42)	78% (45)	100% (42)	100% (44)
latrans	79% (43)	78% (60)	57% (60)	97% (60)	100% (60)
lestes	88% (94)	77% (121)	69% (119)	93% (125)	100% (123)
incolatus	100% (23)	93% (29)	65% (29)	100% (29)	100% (29)
Total LATRANS	89% (250)	77% (315)	71% (318)	96% (319)	100% (320)

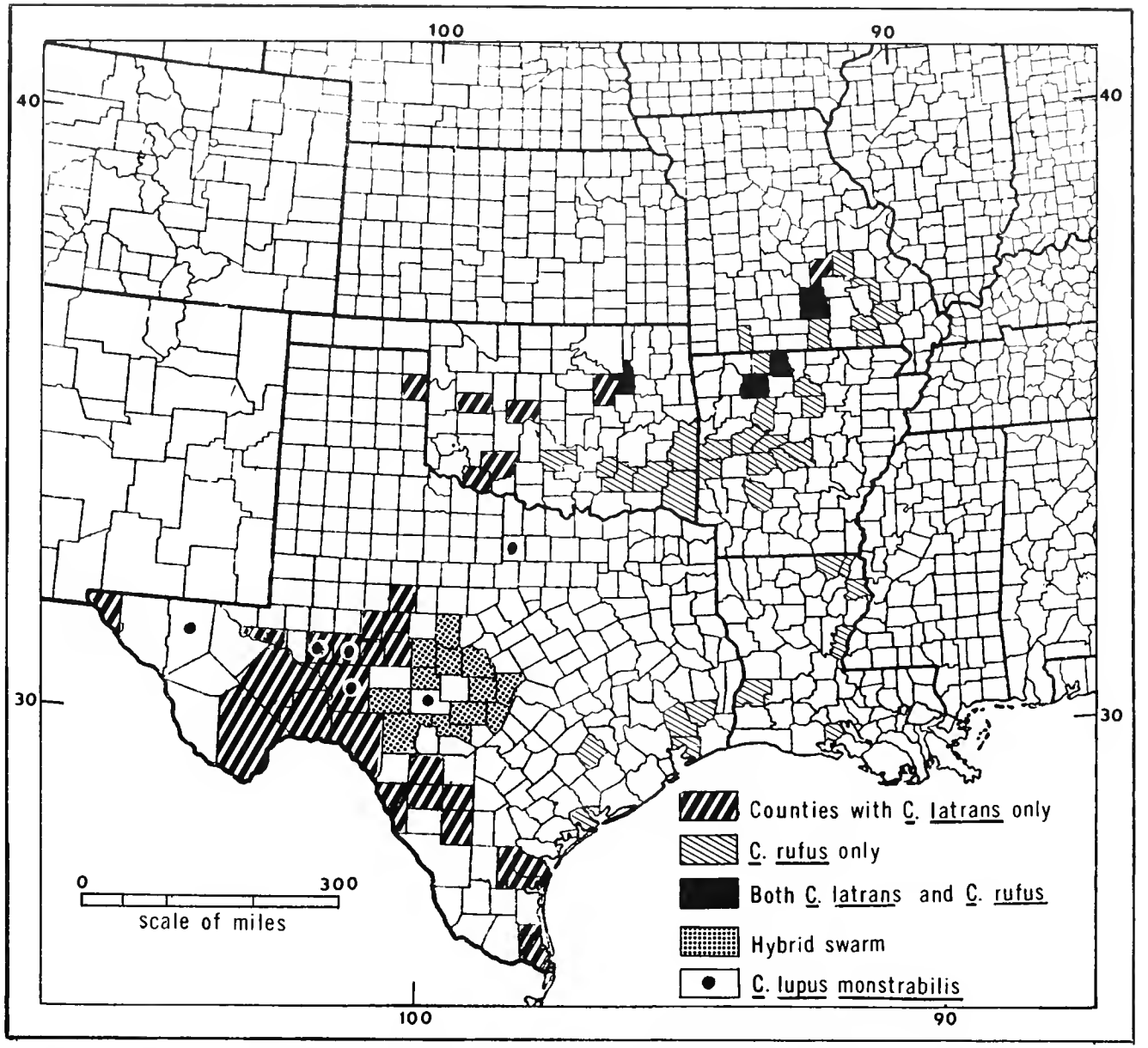

Figure 1.--Distribution by county of canid specimens in the south-central United States before 1930.

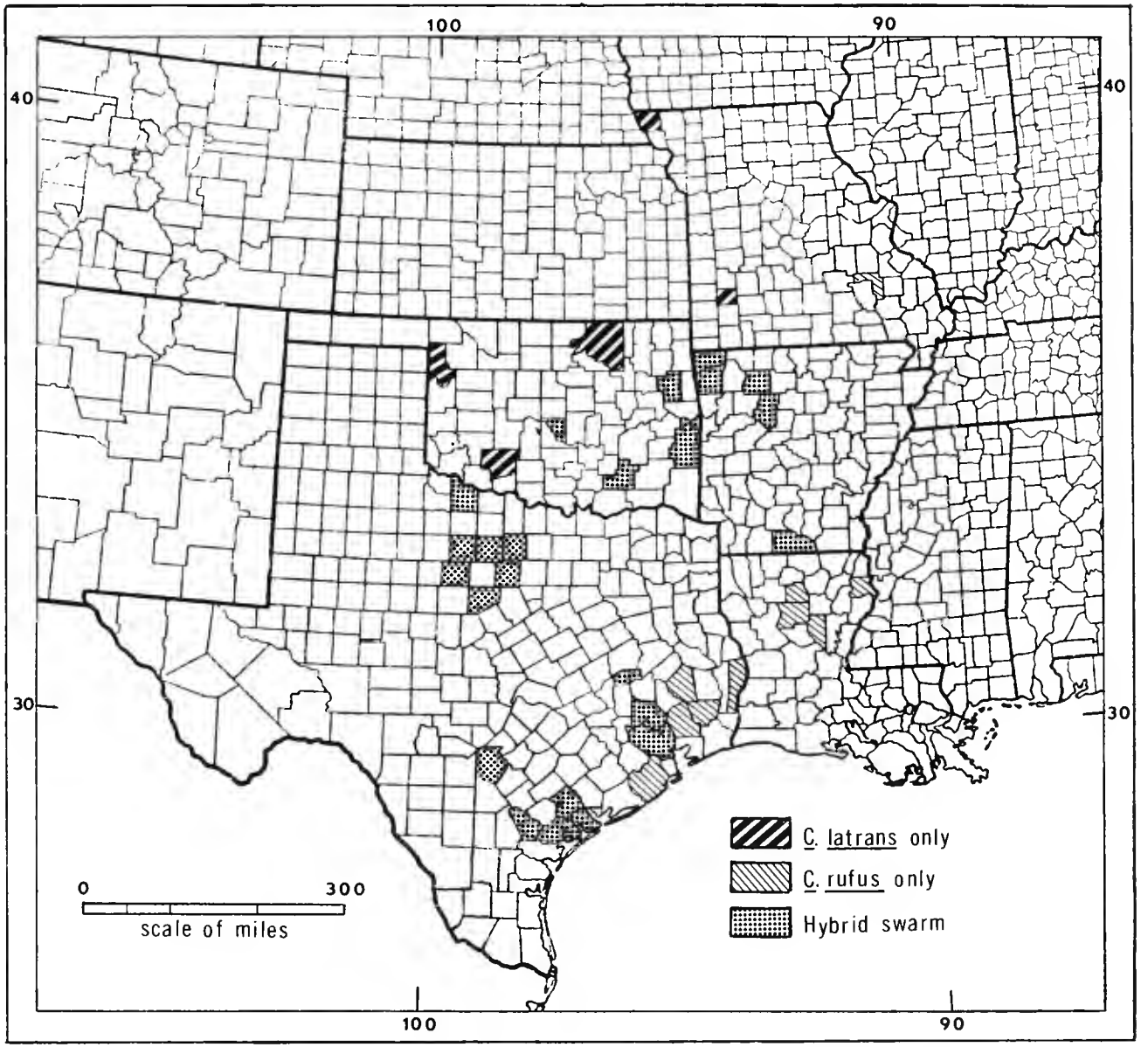

Figure 2.--Distribution by county of canid specimens in the south-central United States, 1932-42.

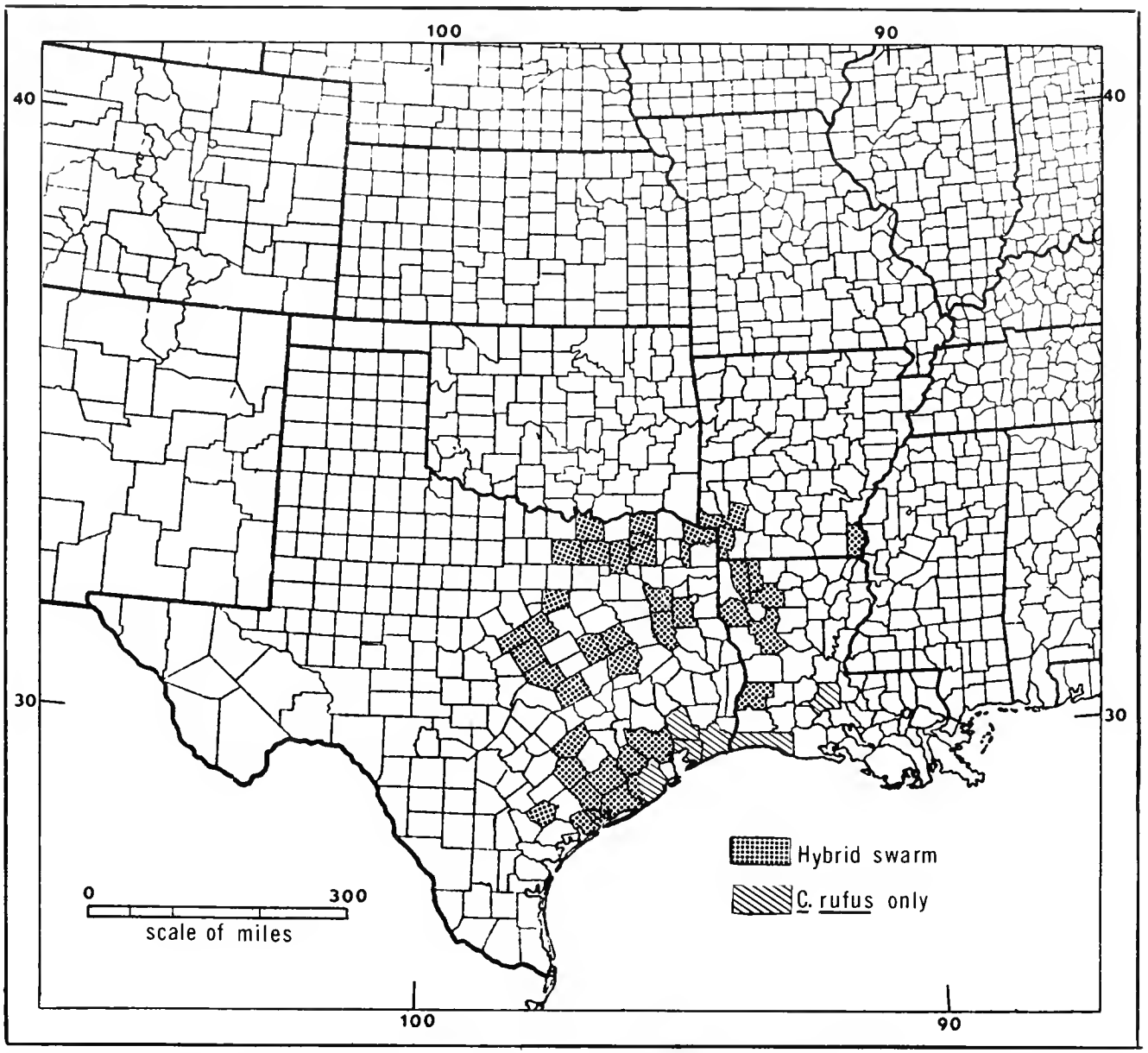

Figure 3.--Distribution by county of canid specimens in the south-central United States, 1963-69.

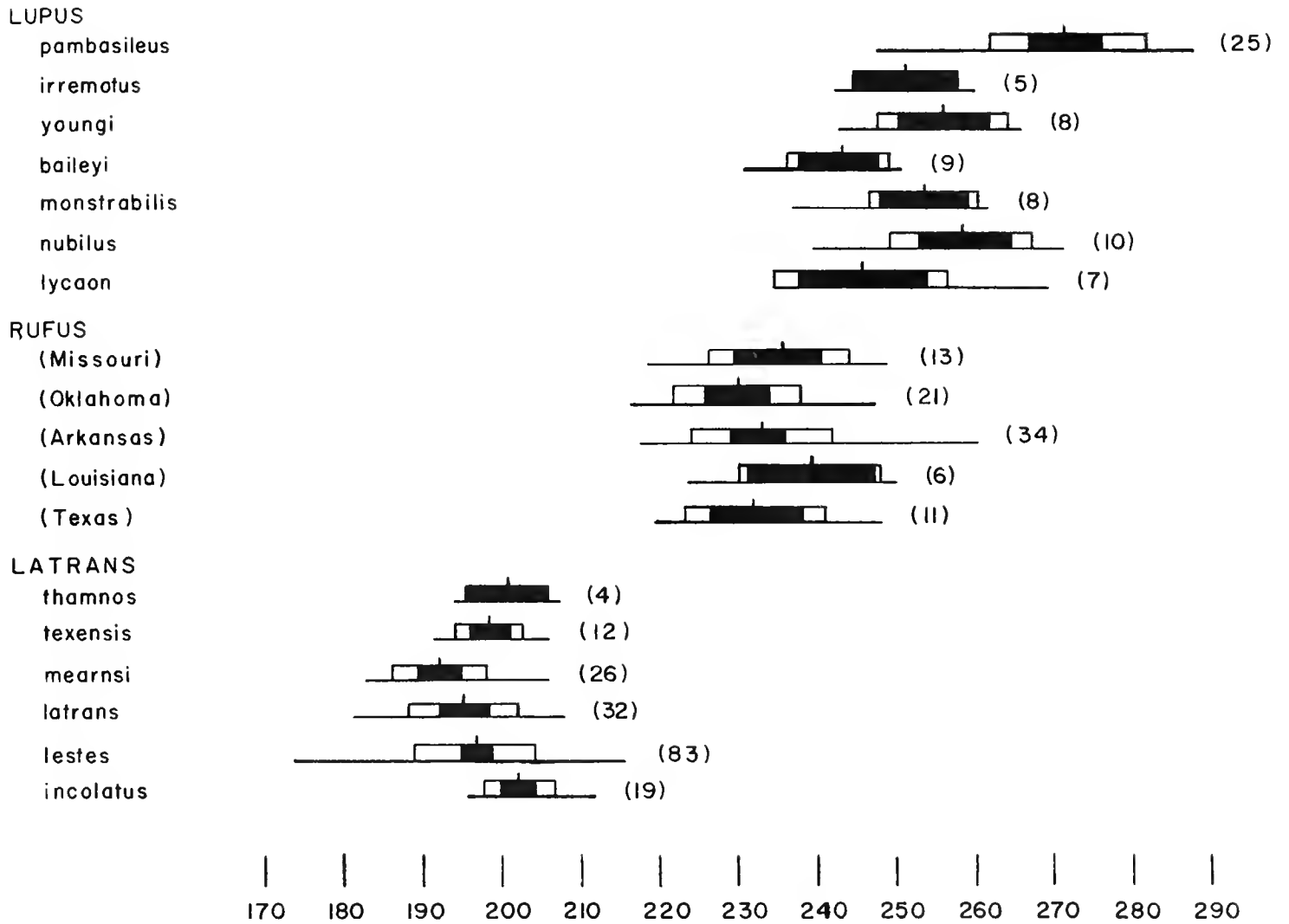

Figure 4.--Standard samples, greatest length of skull in millimeters, males. In this, and all subsequent figures, the slender line represents the range; the black bar indicates two standard errors of the mean on either side of the mean; the black bar plus the white portion on either side indicate one standard deviation on either side of the mean. The mean is indicated by the vertical line on top of the bar; associated numbers refer to sample size.

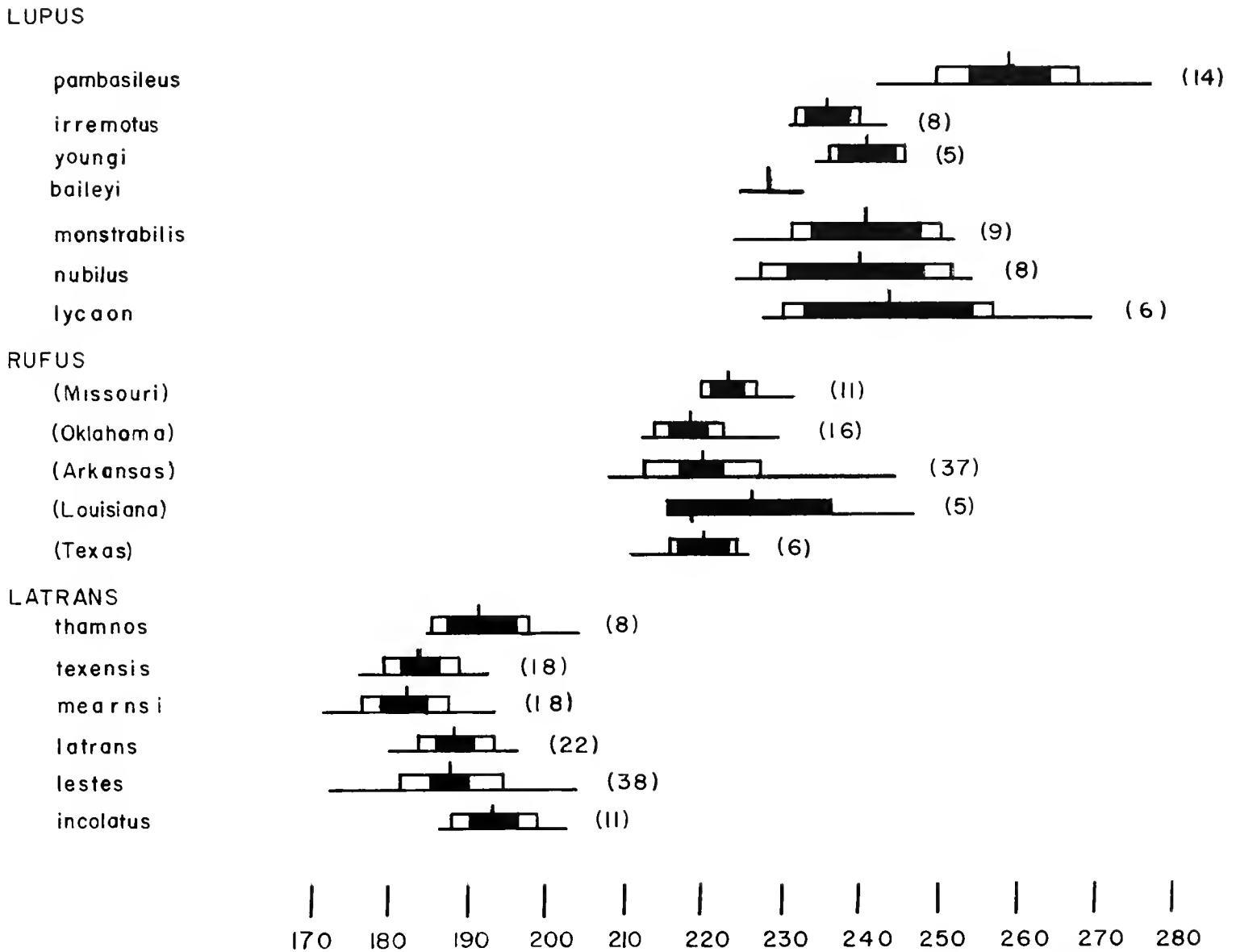

Figure 5.--Standard samples, greatest length of skull in millimeters, females.

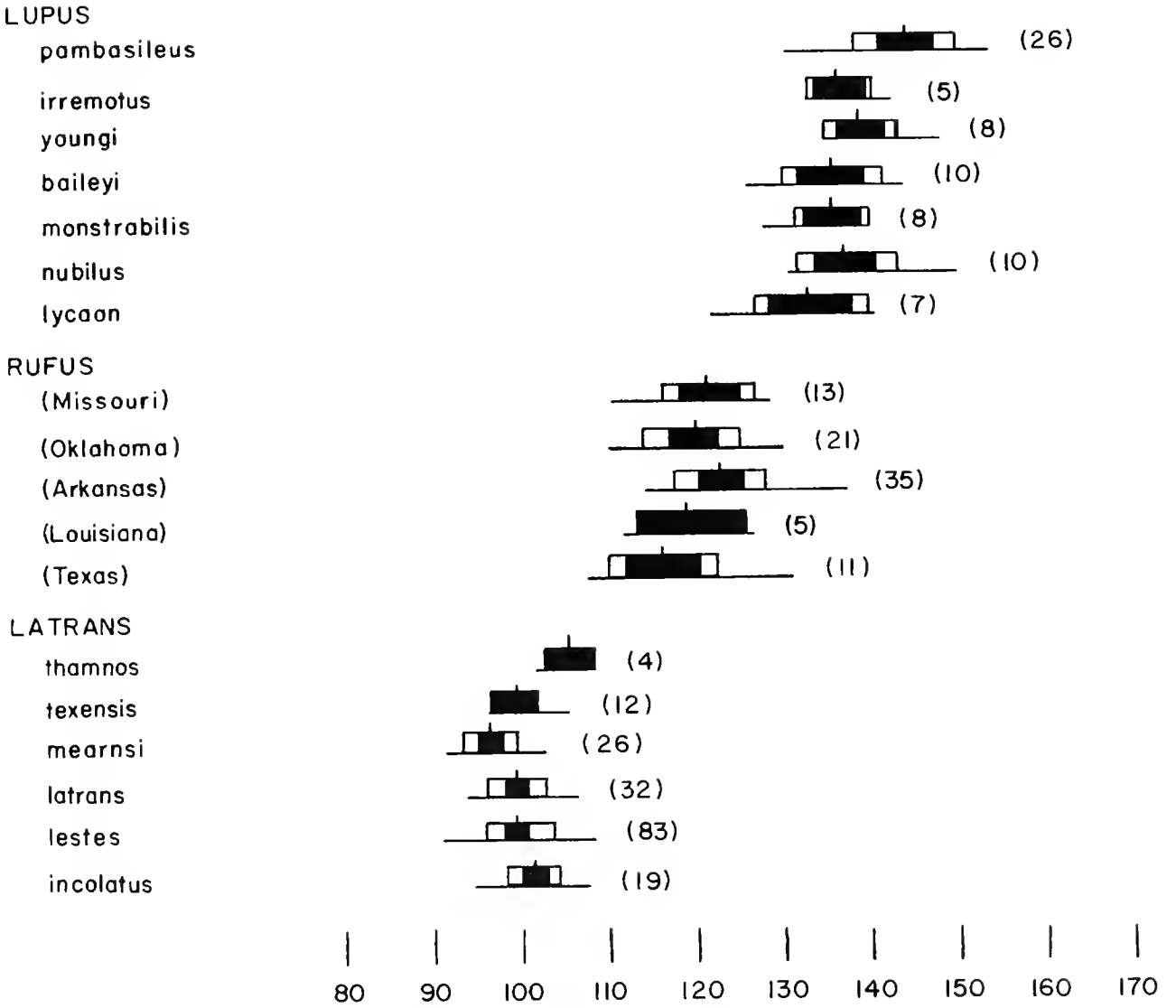

Figure 6.--Standard samples, zygomatic breadth in millimeters, males.

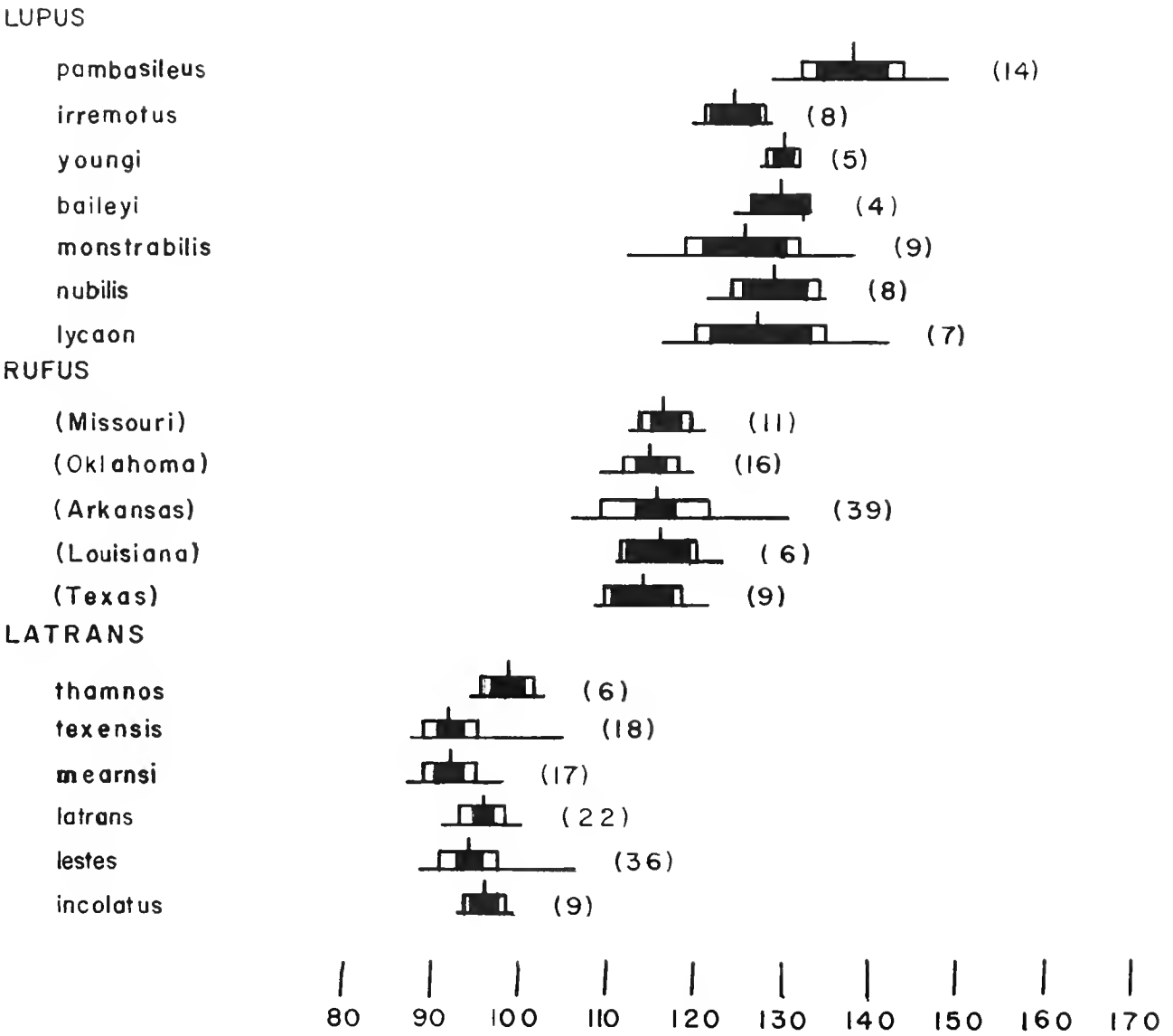

Figure 7.--Standard samples, zygomatic breadth in millimeters, females.

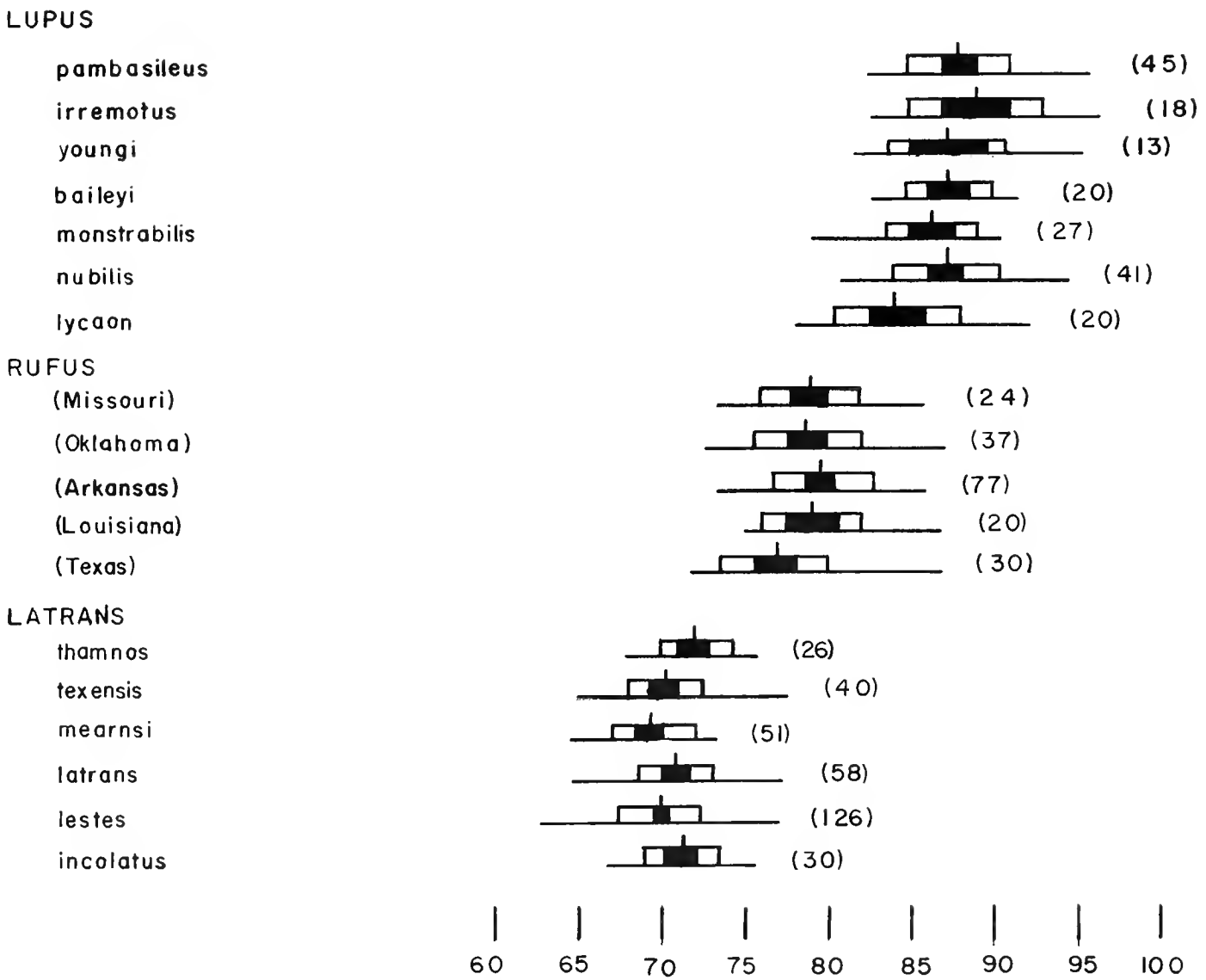

Figure 8.--Standard samples, bite ratio X 100.

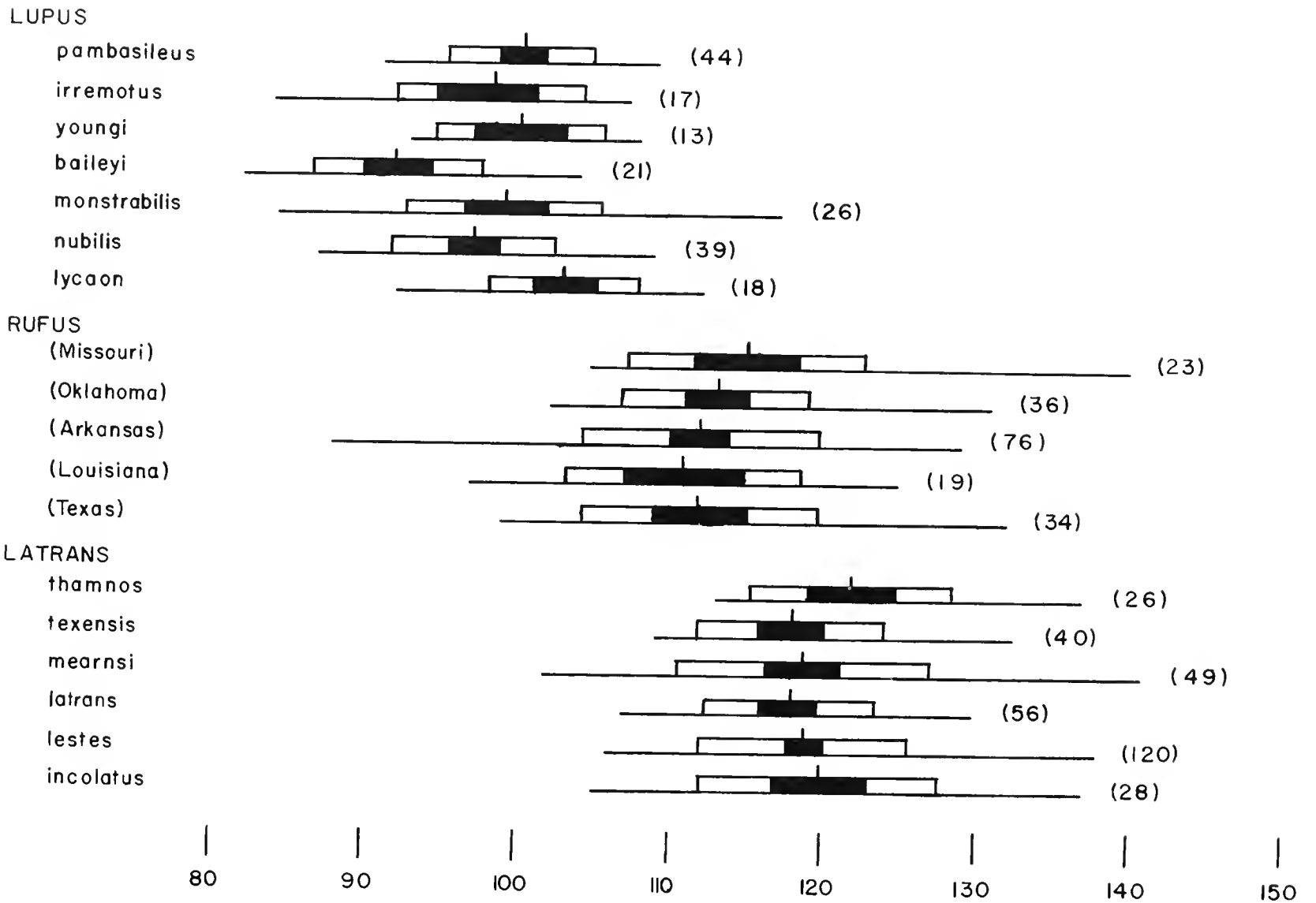

Figure 9.--Standard samples, molar tooth ratio X 100.

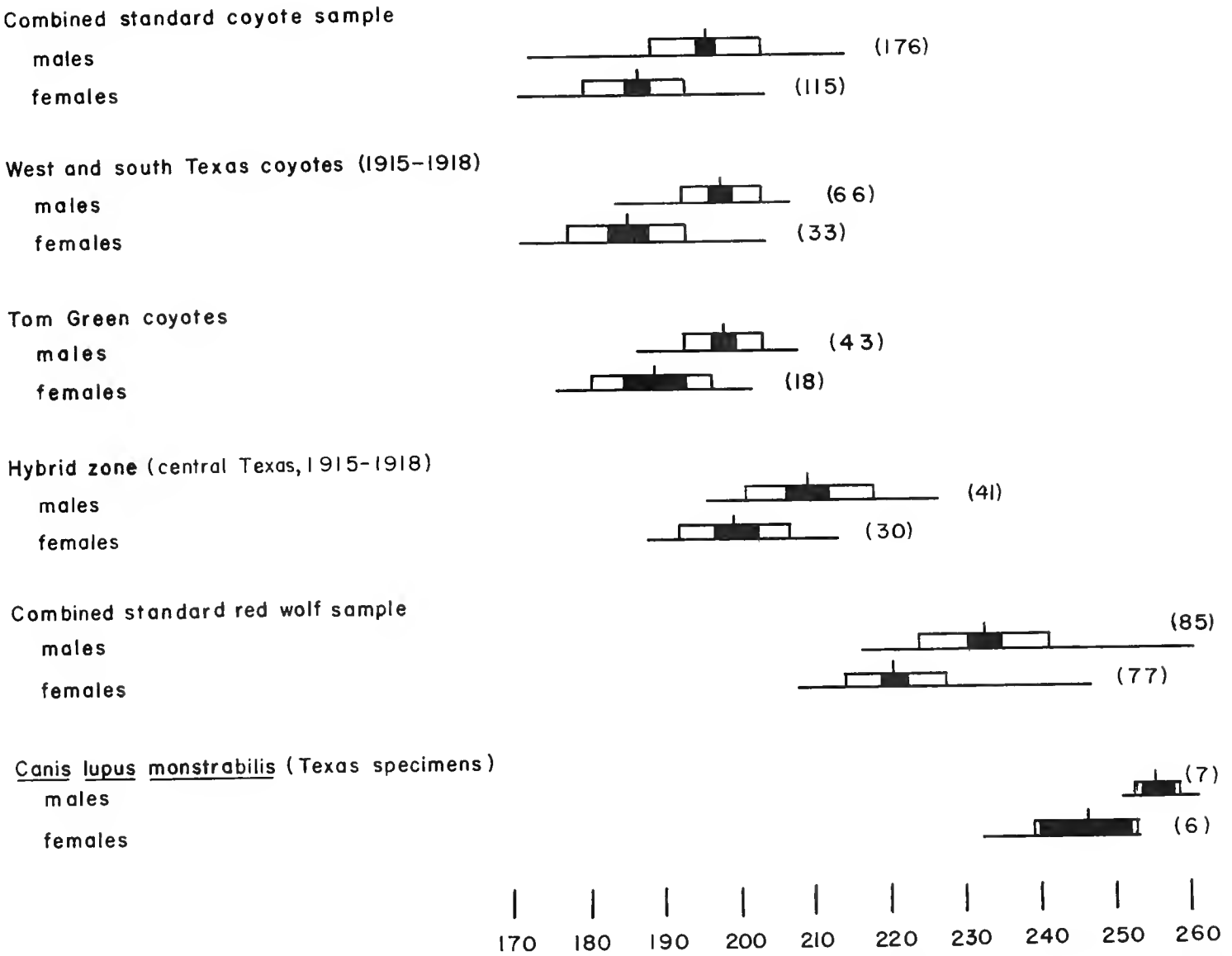

Figure 10.--Greatest length of skull in millimeters, hybrid zone (central Texas, 1915-18) compared with various other canid populations.

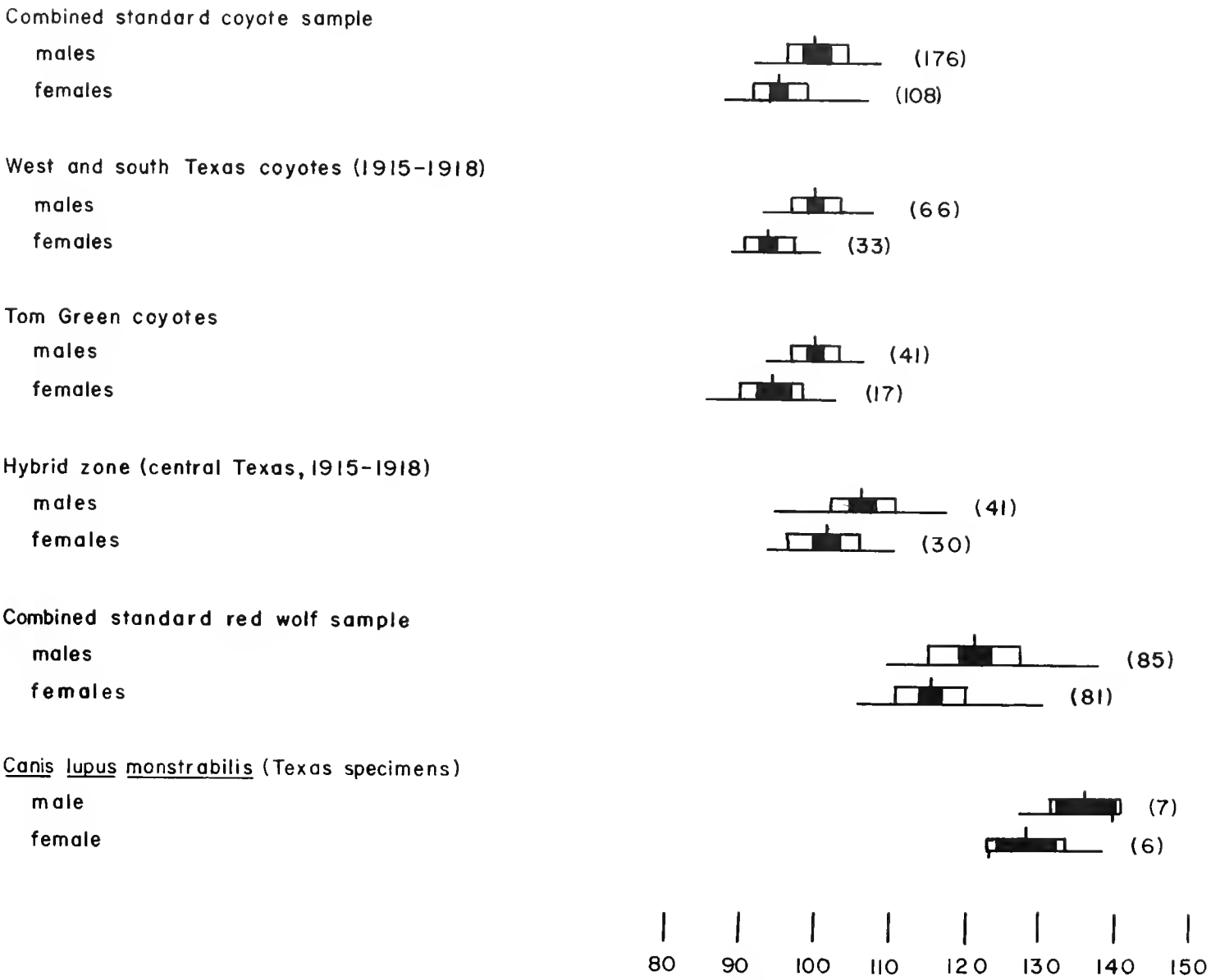

Figure 11.--Zygomatic breadth in millimeters, hybrid zone (central Texas, 1915-18) compared with various other canid populations.

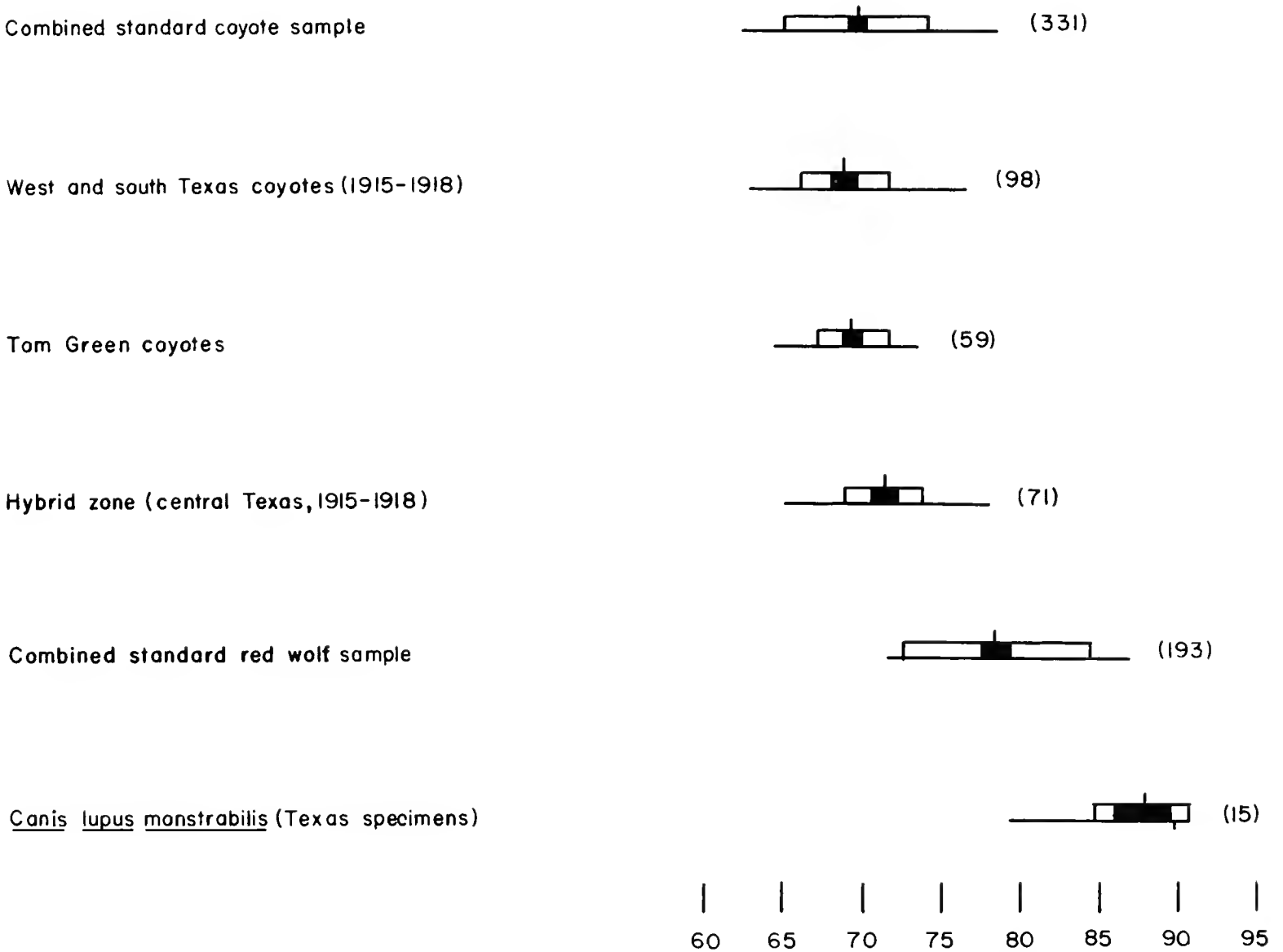

Figure 12.--Bite ratio X 100, hybrid zone (central Texas, 1915-18) compared with various other canid populations.

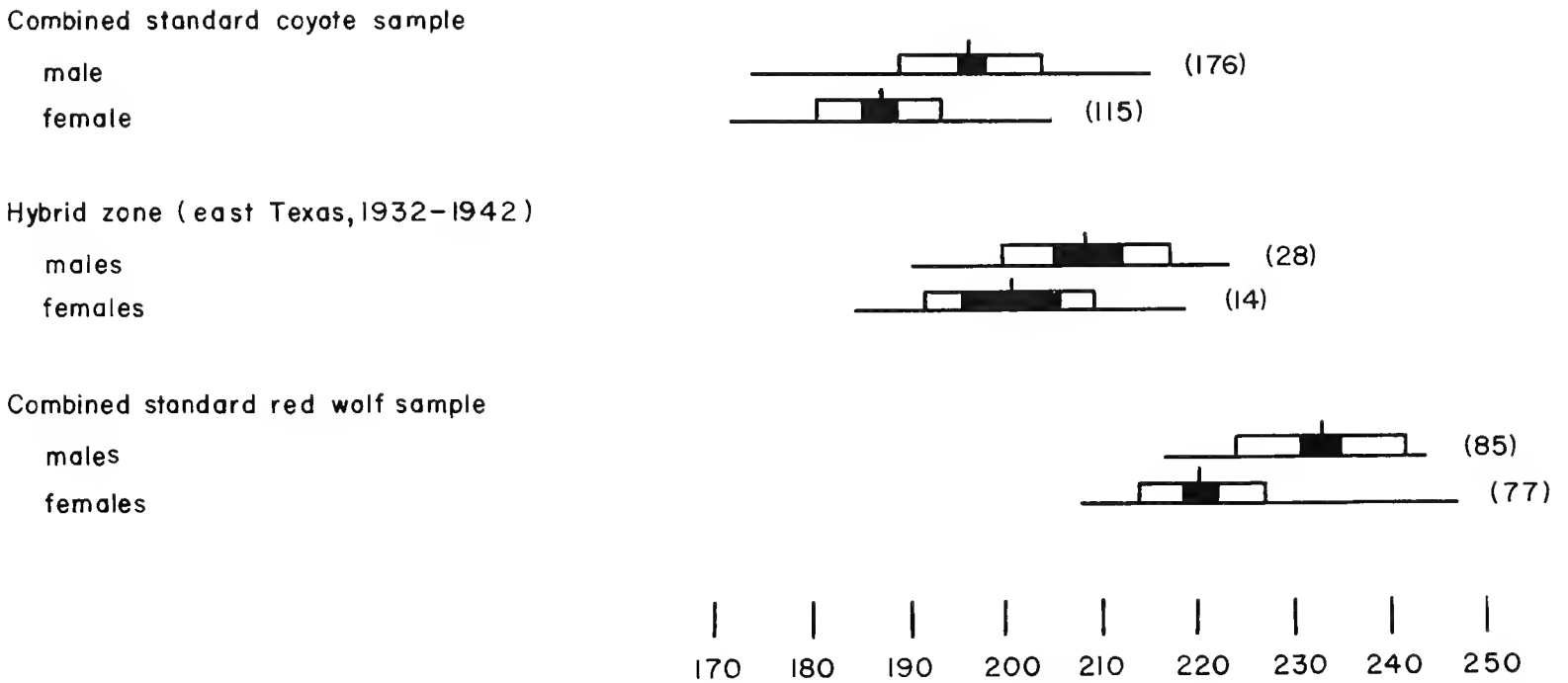

Figure 13.--Greatest length of skull in millimeters, hybrid zone (east-central Texas, 1932-42) compared with various other canid populations.

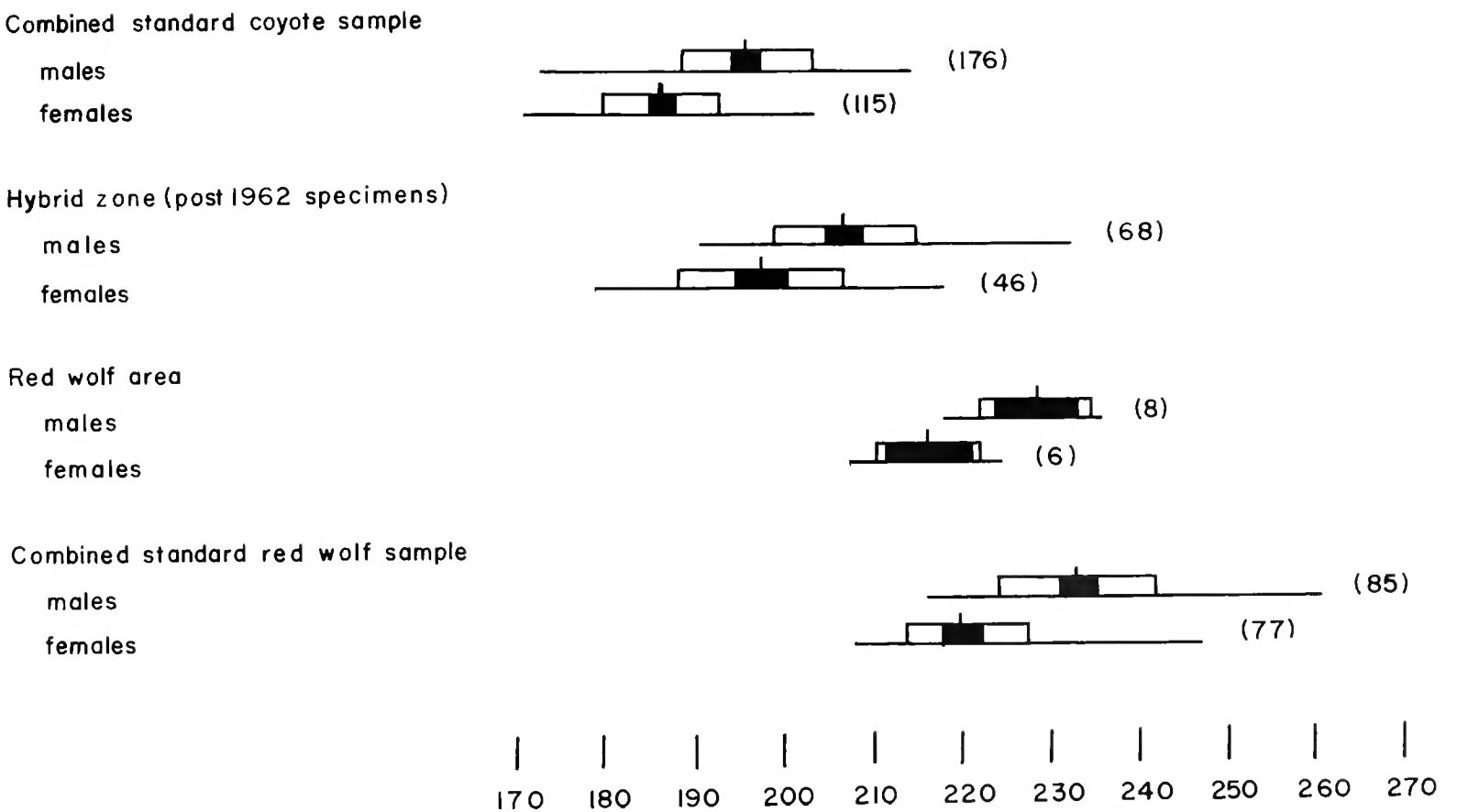

Figure 14.--Canids from the present red wolf area compared for greatest length of skull in millimeters with various other canid populations.

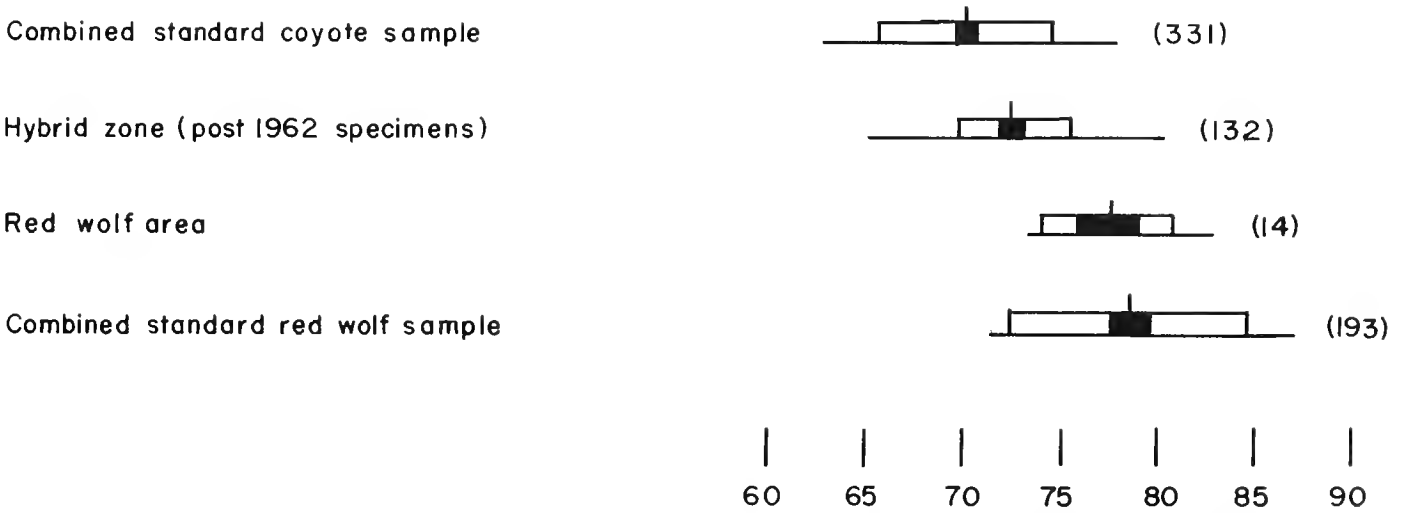

Figure 15.--Canids from the present red wolf area compared for bite ratio X 100 with various other canid populations.

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